

THE CENTRIFUGAL PATTERN OF SPECIATION IN MEGANESIAN RAINFOREST MAMMALS

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The usual model of speciation adopted for mammals is the peripheral population model, a mode of allopatric speciation. Analysis of some patterns of taxonomy in rainforest mammals in the Meganesian ("Greater Australia") region shows, on the contrary, that the more derived taxa — both species and subspecies — tend to occur in the central parts of the distributional area, the more primitive ones at the periphery. This finding seems to support the Centrifugal Speciation model of W.L. Brown, a sympatric mode. An example from Africa is also given, to demonstrate that the centrifugal model is not a local nor a habitat-specific one, but has more general applicability.

□ *Biogeography, Dendrolagus, Meganesia, New Guinea, centrifugal speciation, sympatric speciation, colour pattern.*

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The taxonomist is often accused of working haphazardly, revising a group that happens to be of current interest, without a philosophical aim: mere stamp-collecting, it has been called, and if so then the charge is true, for philately will get us nowhere. This is not to say that essential basic information does not emerge from a taxonomic study, and certainly biology could not progress without taxonomy.

The other side of the coin is the search for patterns. A reviser who is awake is bound to wonder whether his or her new information is forming part of a pattern, and taxonomists make some of the best biogeographers.

This paper will describe a pattern which one taxonomist has found, and discuss whether it has any significance. Crucial to the study were the tree-kangaroos, genus *Dendrolagus*, of which one extant species, *D. bennettianus*, was first described by C.W. de Vis (1886), whom this symposium honours. Other examples are drawn largely from the mammals of Meganesia (for this term, see Filewood, 1984).

SPECIES AND SUBSPECIES IN MEGANESIAN RAINFOREST MAMMALS

The Tree-Kangaroos (*Dendrolagus*) are typical Meganesian rainforest mammals, ranging over most of the New Guinea mainland (with a gap in Irian Jaya, perhaps resulting from a lack of

collecting and observation rather than from a lack of tree-kangaroos), into at least one offshore island, and the Tablelands rainforests of northern Queensland. In a recent revision (Groves, 1982) it was found that the various taxa can be sorted, using mainly characters of the feet and the teeth, into three grades from most primitive to most derived, distributed as follows:

— the primitive long-footed species, namely *D. inustus*, recorded from the whole of Cenderawasih, the Bird's Head peninsula, Yapen Island, and a strip of the northern New Guinea coast; and the two



FIG. 1. Distribution of species-groups in *Dendrolagus*.

- Primitive long-footed group (*inustus*; + *lumholtzi* and *bennettianus* in Australia)
- ▨ Short-footed, narrow-toothed (*matschiei* group)
- Short-footed, broad-toothed (*D. dorianus*)



FIG. 2. Distribution of taxa of the *Dendrolagus matschiei* group.






-  Primitive taxa with no golden markings (*ursinus*, *spadix*)
-  Taxa with slightly developed golden markings (*goodfellowi*, *buergeri*)
-  Taxa with extensive golden markings (*shawmayeri*, *matschiei*)



FIG. 3. Distribution of subspecies of *Dendrolagus dorianus*.

-  Primitively dull-coloured subspecies (*dorianus*, *mayri*)
-  Brightly coloured subspecies (*notatus*)

Queensland species, *D. lumholtzi* and *D. bennettianus*.

— intermediate short-footed species, with little-modified, narrow teeth (especially the secator, P); these are *D. ursinus*, known only from the eastern side of Cenderawasih, and the *D. matschiei* group (including so-called *D. goodfellowi*, as well as *D. spadix* which may be a distinct species), found over most of mainland Papua New Guinea.

— a highly derived, extremely short-footed species, with broad and complex P³, *D. dorianus*, which seems to be found only in the highlands, from far southeastern Papua westwards into Irian



FIG. 4. Distribution of species-groups in *Dorcopsulus*.





-  Primitive taxa, with long feet and long secator (*vanheurni* group)
-  Derived taxa with short feet and shortened secator (*macleayi* group)



FIG. 5. Distribution of taxa in *Microperoryctes*.

-  Primitive taxa: duller colour without strong contrasts (*longicauda*, *dorsalis*, *murina*, *papuensis*)
-  Derived taxa: brightly coloured with strong contrasts (*ornata*, *magna*)

Jaya, with an isolated(?) population in the Wondiwoi peninsula. It does not extend into the Huon peninsula, nor into the hilly regions of the south coast.

Looking at the ranges of these three species-groups (Fig. 1), it is evident that the primitive group occurs on the western, northern and southern extremities of the distribution of the genus (and is the only one on an offshore island; *D. matschiei*, on Umboi I., is probably introduced). The highly derived *D. dorianus* has the most central distribution; the intermediate group has an intermediate range.

The subspecies/species within at least two of these groups show a similar pattern. In the *D. matschiei* group, the most strikingly marked taxa occupy the central portion of the group's range

(Fig. 2). In *D. dorianus* it is again the most brightly coloured, most metachromatically advanced, subspecies which is centrally distributed (Fig. 3).

In collaboration with T.F. Flannery (Australian Museum), I am working on revisions of certain other rainforest marsupials; a progress report on two genera is given here. *Dorcopsulus* — the dwarf, montane forest wallabies — can probably be divided into several species, constituting a primitive and a relatively derived group. The more primitive taxa, with long feet and long narrow P³, occur from the Idenburg River region east to the Huon peninsula, and recur in southeastern Papua. Between these two ranges — and, as far as we know, allopatric to either — is found the highly derived *D. macleayi* group (Fig. 4).

For the New Guinea Striped Bandicoots, genus *Microperoryctes* (which includes some taxa transferred from *Peroryctes* — see Groves & Flannery, in press), we have again incomplete distributional data. Even so, we again appear to have a highly derived group — bright yellow with well-marked black dorsal, face and rump stripes — occurring between the ranges of duller, less disruptively marked (metachromatically more primitive) taxa (Fig. 5).

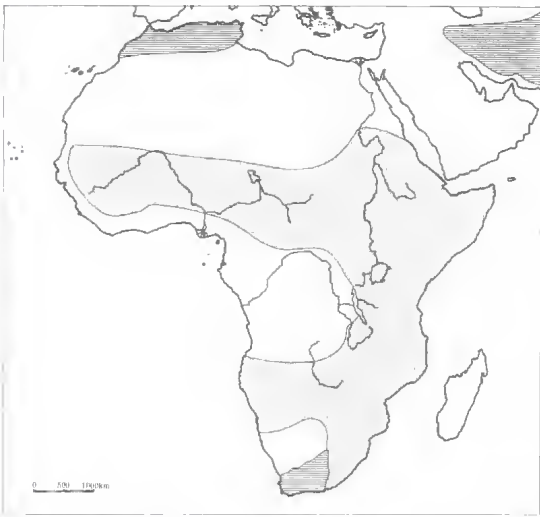




FIG. 6. Distribution of subspecies-groups in *Panthera leo*.

-  Primitive, small-brained subspecies (*leo*, *persica*, *melanochaita*)
-  Derived, large-brained subspecies (*senegalensis*, *nubica*, etc.)

ANALOGOUS PATTERNS OUTSIDE MEGANESIA

The immediate question must be: is this pattern coincidental, or is it a more widespread phenomenon? Does it occur only in Meganesia? Or is it something to do with a rainforest habitat?

It turns out that the pattern is neither specific to this particular region, nor is it limited to the rainforest environment. On the contrary, it is a common distributional pattern, which has sometimes been noticed and commented upon by taxonomic revisers who have worked on groups which exhibit it. Thus Hemmer (1974) found that the Lion (*Panthera leo*) can be divided into two subspecies-groups: a primitive one with relatively small cranial capacity, and a more evolved one in which cranial capacity is greater, the male's mane is more heavily concentrated around the head-pole, and social organisation is more complex. The derived group is common to most of Sub-Saharan Africa, while the primitive group is dotted around the periphery — the Cape of Good Hope, the Maghreb, and southwestern Asia (Fig. 6).

THE CENTRIFUGAL MODEL

Brown (1957) named this pattern 'centrifugal speciation'. According to his model, genetic novelties are generated in the centre of a species' range, and subsequent climatic changes break up the range, providing the opportunity for allopatric speciation to occur, leaving primitive taxa around the edges while a new, more derived species has evolved in the centre.

Brown's model remained little appreciated, but was briefly discussed by White (1978), who, however, rejected it. It seems to me that, in modified form, centrifugal speciation explains patterns of taxonomic differentiation such as I have described above. Moreover, from a population genetic point of view, it would seem so obvious as to be almost the expected mode of taxonomic advance.

As demonstrated by the above examples, the centrifugal pattern applies to subspecies as well as to species, and, indeed, to polymorphisms as well (Groves, 1989). Lewontin (1974) emphasises that the sorts of characters that differentiate species are the same as those subject to polymorphism or polytypism within a species, indeed they are often the same characters. *Contra* the ideas of the proponents of rectangular speciation (Stanley, 1979), there is no fundamental difference between the kinds of variation distinguishing species,

subspecies, and even sub-taxonomic degrees of variation: only in species the differentiation is accompanied, due to whatever mechanism, by reduction or loss of interfertility.

Brown's appeal to range changes, to create opportunities for allopatric speciation, may be unnecessarily cumbersome. As long ago as 1966, Maynard Smith proposed a viable mechanism for sympatric speciation; to which White added the stasipatric mode, where there is a chromosomal rearrangement leading in effect to a high degree of inbreeding. I cannot insist on sympatric speciation as part of the revived centrifugal model, but I will point out that, viewed as a package, the two concepts make sense together:

- 1) the package is geographically parsimonious;
- 2) breeding systems regularly promote the wide dissemination of mutations and recombinations;
- 3) only a "minute fraction" (White, 1978) of all individuals of a species, and so a minute fraction of the genetic diversity, is geographically peripheral; and
- 4) central environments are likely to be more diverse than peripheral, so a new species or morph generated there is more likely to be successful.

HOW COMMON IS CENTRIFUGAL DIFFERENTIATION?

I have elsewhere (Groves, 1989) surveyed patterns of taxonomic differentiation among Primates, and have found 34 instances of clearly expressed centrifugal patterns. Of these, 26 cases involve full speciation, where the generation of new characters has involved the generation of reproductive isolation as well. On the other hand there are only 14 clear cases (plus four more probable) of allopatric speciation.

Of the 26 cases of evident centrifugal speciation, only eight are clearly stasipatric, i.e. involving chromosomal changes. Moreover, breeding systems with inbreeding potential are involved in

only two of the eight stasipatric cases, contrary to the arguments of Bush *et al.* (1977).

Those cases where an allopatric mode best explains the speciation pattern concern genera ranging over two or more major biome-types, whereas in the centrifugal list there are no such cases. The implication would seem to be that if there are habitat differences then adaptation (or exaptation?) will occur; if not, then evolution will proceed just the same, non-adaptively, by centrifugal processes.

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